Foliar and shoot allometry of pollarded black locust, Robinia pseudoacacia L.

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Abstract

Browse of multipurpose tree species such as black locust could be used to broaden grazing options, but the temporal distribution of foliage has not been adequately studied. Our objective was to determine effects of harvest date, P fertilization (0 and 600 kg ha⁻¹ yr⁻¹), and pollard height (shoots clipped at 5-, 50-, and 100-cm above ground) on foliar and shoot allometry of black locust. The experiment was conducted on a naturally regenerated 2-yr-old black locust stand (15,000 trees ha⁻¹). Basal shoot diameter and foliar mass were measured monthly in June to October 2002 and 2003. Foliar and shoot dry mass (Y) was estimated from basal shoot diameter (D) by the function $Y = aD^b$, with regression explaining $\geq 95\%$ of variance. Allometry of foliar mass was affected by harvest date, increasing at a greater rate with D in September than in June or July, but not by P fertilization or pollard height. Foliar mass was predicted best by month-specific equations for the June to October growth interval. Allometry of shoot dry mass was unaffected by harvest date, P fertilization, or pollard height. These equations could be used as a first approximation of foliar and shoot mass for pollarded black locust.

Introduction

Variations in summer rainfall (Hu 2002) can cause localized water deficits that constrain yields of C₃ and C₄ herbaceous forages, and require supplemental hay feeding to sustain livestock. Producers could substantially increase profit margins by developing forage systems that extend the grazing season, thus decreasing or eliminating the high costs of harvesting and feeding hay during these dry periods. Multipurpose trees could have a particular niche for rotational livestock browse when drought limits forage options and livestock productivity, as has been demonstrated for temperate (Oppong et al. 2002) and

sub-Mediterranean regions (Papanastasis et al. 1998). However, the browse potential of multipurpose tree species and the temporal distribution of foliar biomass need further study.

Black locust is a rapid-growing, N₂-fixing, multipurpose species native to the USA (Bongarten et al. 1992) that could be integrated with herbaceous species for livestock production. Depending on row configuration, black locust yielded 900–5000 kg dry matter ha⁻¹ yr⁻¹ of pruning (foliage plus shoot) biomass in Oregon, USA (Seiter et al. 1999). In west-central Arkansas, USA, black locust yielded as much as 5300 kg dry matter ha⁻¹ when harvested in August (Burner et al. 2005), while the

herbaceous grasses *Festuca arundinacea* Schreb. and *Cynodon dactylon* L. harvested monthly normally yield about 1000 kg ha⁻¹ in August (Baker 2000; Burke et al. 2004). Fodder of black locust has excellent nutritive value (≥170 and 534 g kg⁻¹ for crude protein and digestibility, respectively) that meets or exceeds maintenance needs for *Bos taurus* L. (Burner et al. 2005).

Precipitation, competing vegetation, and soil N were the best predictors of aboveground biomass of black locust in short rotation plantations in the central Great Plains, USA (Converse and Betters 1995). Estimates of foliar mass are needed to optimize livestock stocking and rotation intervals, but foliar mass of trees is more difficult to measure than that of herbaceous forages. Direct biomass measurements are destructive and time-consuming, but biomass may be estimated indirectly and non-destructively using an easily measured tree dimension such as stem diameter as the predictive variable (Perttunnen et al. 1996).

It may be possible to develop allometric equations to predict foliar mass of black locust for silvopastoral plantations. A study of seven woody browse species demonstrated that foliar and shoot biomass were predicted ($R^2 = 0.16$ –0.76) from stem diameter using a combination of equations, with predictions usually $\pm 20\%$ of actual values (MacCracken and van Ballenberghe 1993). However, shoot diameter accurately predicted shoot biomass, but not foliar biomass, for four of six woody shrubs clipped to simulate browsing (Pitt and Schwab 1990).

Tree age (Niklas 1995), fertilization (Heinsoo et al. 2002), pollarding (Oppong et al. 2002), and spacing (Verwijst and Telenius 1999) can have mitigating, species-specific effects on tree allometry. Black locust and other tree species exhibited size-dependent allometry in which the scaling exponents of tree height, diameter, and trunk taper progressively change with tree age (Niklas 1995). Similarly, 1-, 3-, and 4-yr-old Salix viminalis L. shoots had increasingly greater dry mass at a given diameter (Heinsoo et al. 2002). Fertilization with N, P, and K affected allometry of shoot biomass productivity by reducing shoot dry weight compared to non-fertilized shoots (Heinsoo et al. 2002). Fertilization of black locust seedlings with P and K increased foliar and shoot biomass when soil concentrations of available P and K

were ≤ 3.5 and 63 μ g g⁻¹, respectively (Pope and Andersen 1982).

Pollard initiation date and pollard frequency affected aboveground dry matter partitioning and leaf-stem ratio of two Salix species in New Zealand (Oppong et al. 2002). Pollarding increased the number of meristematic foci and shoot initiation, but reduced shoot biomass of Eucalyptus kochii Maiden & Blakely subsp. plenissima Gardner (Brooker) compared to that of uncut trees (Wildy and Pate 2002). However, pollarding did not affect biomass allometry of four tree species (Harrington and Fownes 1993). Effects of pollarding and pruning on allometry may be related to concentrations of reserve carbohydrates (Garcia et al. 2001) or N (Mediene et al. 2002) in unpruned tissues. Our objective was to determine effects of harvest date, P fertilization, and pollard height on foliar and shoot allometry of black locust.

Materials and methods

The study was conducted near Booneville, Arkansas, USA (35°05′ N, 93°59′ W, 152 m a.s.l.) on a Linker fine, sandy loam soil (fine-loamy, siliceous, thermic Typic Hapludult). Black locust trees recolonized the site during 2000 and 2001 from existing roots at a stocking rate of about 15,000 trees ha⁻¹. Trees were about 2 m tall at the end of the 2001 growing season (before initiating the study). Plots were 5.5×9 m and trees were examined in 2002 and 2003. We previously reported the biomass production and foliar nutritive value for this study (Burner et al. 2005).

Experimental treatments

The 2-yr study was a split-plot design with two treatments (P fertilization and pollard height) and two replicates. Phosphorus fertilization (0 and 600 kg P ha⁻¹ yr⁻¹) was the main plot effect, and pollard height (dormant shoots clipped in December 2001 to 2003 at 5-, 50-, and 100-cm height above ground) within P fertilization was the subplot effect.

Plants clipped 5 cm above ground surface are actually coppied while plants clipped at 50- and 100-cm height are pollards. For simplicity, however, the term "pollard" will be used for all

clipping treatments. Further, the term "shoot" will be used to designate either the primary stem developing from plants clipped at 5-cm height, or axillary branches that arose from the primary stem in 50- and 100-cm pollard treatments.

Measurements

Once monthly from early June to early October 2002 and 2003, three shoots were selected at random from each plot. The growing season for black locust began with bud-break in early April, so leaves were about 2 mo-old at the June harvest. Leaves normally senesced by mid- to late October. The three shoots were clipped at the same pollard height as that applied to the whole plot. Shoot basal diameter was measured with a caliper 5 cm distal to the clipping height for 5-cm pollards, or 5 cm distal to the branch point for 50- and 100-cm pollards. Shoots of any individual tree were sampled only once yearly, so measurements at any given harvest date represented growth accumulated from the beginning of the growing season. Foliage (petioles and leaflets) was removed from the clipped shoots, including 5-10 cm of unlignified shoot apex. Foliar and shoot samples were dried at 60 °C for 48 and 120 h, respectively. Shoot mass for 5-cm pollards in 2002, and for 50and 100-cm pollards in June and July 2002 was not recorded. Dormant shoots clipped in December 2002 and 2003 from each plot were counted and weighed. Foliar and shoot mass were expressed on a dry weight basis (g shoot⁻¹).

Statistical analysis

Main plot and split plot effects were P fertilization and pollard height within P fertilization, respectively. Normally distributed, *In*-transformed data were subjected to analysis of variance with a mixed linear model (Littell et al. 1996). Fixed effects were harvest date (4 df), P fertilization (1 df), pollard height within P fertilization (4 df), and the interactions harvest date×P fertilization (4 df) and harvest date×pollard height within P fertilization (16 df). Replication (1 df) and its interactions with fixed effects were considered random effects. Tree density varied among plots, so analysis of variance was conducted with and without a covariance

adjustment (SAS Inst. 1998) for tree density. Pollard height was analyzed as a repeated measure with an autoregressive order 1 covariance structure (Littell et al. 1996). Denominator df were calculated by a general Satterthwaite approximation method (Littell et al. 1996).

Regression analysis of *ln*-transformed data was used to calculate a and b, the intercept and slope of the function, respectively, for each level of treatments (harvest date, P fertilization, and pollard height). The a and b values were the starting parameters for iterative, non-linear analysis of non-transformed data (Freund and Littell 2000). Foliar and shoot mass were calculated for each treatment level with the non-linear equation: $Y = aD^b$, where Y was foliar or shoot mass and D was basal shoot diameter. Slopes for each level of a treatment were compared by approximate 95% confidence limits (Freund and Littell 2000). A combined response was computed across treatments. If slopes differed between levels of a treatment, predicted responses from combined and specific equations were compared by 95% confidence limits. Residuals from combined and specific equations were tested for normality by the Shapiro-Wilk statistic (SAS Inst. 1998).

Results

There was a large range of basal shoot diameter and foliar and shoot mass for pollarded trees (Table 1). Use of tree density as a covariate did not alter interpretations of F-tests for mean squares of foliar and shoot mass (data not shown). The interaction of harvest × P fertilization was not significant for basal shoot diameter or mass $(p \ge 0.64)$. The interaction of harvest \times pollard height within P fertilization was significant for basal shoot diameter (p = 0.03), but not for foliar or shoot mass $(p \ge 0.11)$. Basal shoot diameter and mass were affected by simple effects of harvest date pollard height within P fertilization $(p \le 0.001)$. Basal shoot diameter and foliar mass $(p \le 0.03)$, but not shoot mass (p = 0.06), were affected by P fertilization.

Allometry of foliar dry mass was affected by harvest date (Table 2), but not by P fertilization or pollard height ($p \ge 0.05$, data not shown). Foliar mass increased very little across the limited range of basal shoot diameter in June, compared to

Table 1. Mean basal shoot diameter, foliar dry mass, and shoot dry mass for pollarded Robinia pseudoacacia in Arkansas, USA.

Variable	N	Mean \pm s.e.	Range
Basal shoot diameter (mm)	360	18.8 ± 0.27	5.8-35.6
Foliar dry mass (g)	360	135.5 ± 4.14	23.2-408.5
Shoot dry mass (g)	276	222.1 ± 9.07	14.0–908.7

subsequent months (Figure 1). Further, foliar mass (Table 2) increased with D at a greater rate in September than in June or July ($p \le 0.05$). Residuals from combined and month-specific equations for harvest date were normally distributed, except for foliar mass in June ($p \ge 0.05$, data not shown). Explained variance was similar for combined and month-specific equations. Predicted values for combined and specific equations deviated significantly for June and July, but not for August to October.

Treatments did not affect allometry of pollarded shoot mass ($p \ge 0.05$, data not shown). Shoot mass was described by the equation, $Y = 0.0427D^{2.8709}$, which explained 98% of the variation.

Discussion

The prediction of foliar mass would be facilitated using combined, rather than treatment level-specific equations. Generalized equations that deviate <10% (Verwijst and Telenius 1999) or even <20% (Dudley and Fownes 1992) from specific equations may be acceptable depending on stringency of the margin of error. However, slopes differed with harvest date, mean deviations for month-specific and combined equations differed for the June and July growth interval, and mean

deviations for July and October were >20% (Table 2).

Dry mass at any given month accumulated from the beginning of the growing season. The temporal allometric responses probably reflected a change in plant architecture or assimilate allocation during the growth trajectory (Verwijst and Wen 1996), although those traits were not measured. Progressive, age-related changes in allometry of un-pruned trees are the result of the ontogenic transition from primary to secondary growth (Niklas 1995). Besides its acute affects on foliar architecture, pruning has more subtle effects on assimilate repartitioning (Garcia et al. 2001; Mediene et al. 2002; Perttunnen et al. 1996). While pollard height treatments removed different quantities of dormant R. pseudoacacia biomass, and presumably storage carbohydrates (Magel et al. 1994), there appeared to be negligible effect on subsequent dry matter partitioning to shoots. Black locust recovered rapidly following pruning. Some hardwood tree species with resprouting capacity recover slowly following pruning (Wildy and Pate 2002), while others recover rapidly after pruning (Garcia et al. 2001; Oppong et al. 2002) by shifting carbohydrate reserves from branches to basal tissues (stem and roots). Nutrient differentials may also affect foliar (Harrington and Fownes 1993) and shoot allometry (Heinsoo et al. 2002).

Table 2. Allometric responses of foliar dry mass (g shoot $^{-1}$) of Robinia pseudoacacia (Y) as a function of basal shoot diameter (D, mm) in Arkansas, USA.

Harvest date	Equation	Test of slope ^a	RMS ^b	Explained variance (%)	Deviation ^c (%)
June	$Y = 9.4976 \ D^{0.6638}$	c	88.7	97	15.4 ^d
July	$Y = 0.5769 D^{1.9305}$	b	139.5	99	21.6 ^d
August	$Y = 0.3054 D^{2.1083}$	ab	637.3	98	15.4
September	$Y = 0.0126 D^{3.0142}$	a	877.6	97	14.1
October	$Y = 0.0873 D^{2.3899}$	ab	178.9	99	23.9
Combinede	$Y = 0.5781 \ D^{1.8451}$		1177.6	95	

^aFunction slopes (exponents) with a common letter did not differ at $p \le 0.05$.

^bRMS = residual mean square.

^cMean deviation of predicted responses for combined and specific equations.

^dMean deviation for combined and specific equations differed at $p \le 0.05$.

^eCombined across harvest dates.

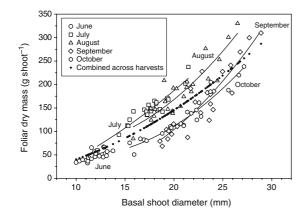


Figure 1. Relationship of foliar dry mass to basal shoot diameter for June to October harvests, and combined across harvests, for *Robinia pseudoacacia* in Arkansas, USA.

The lack of a P fertilizer response suggested that concentrations of available soil P (67.8 μ g g⁻¹) were not limiting for black locust growth (Burner et al. 2005; Pope and Andersen 1982).

Basal shoot diameter of pollarded black locust was predictive of foliar and shoot mass. Because of its sensitivity to harvest date, foliar biomass in June and July was best described by month-specific equations. This was important because of the potential for changes in forage availability during the June to October growth interval. Shoot diameter was strongly predictive of shoot biomass independent of harvest date, P fertilization, and pollard height. These equations could be used as a first approximation of foliar and shoot mass for pollarded black locust, assuming that similar cultural practices are applied to the stand.

Notes

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